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The first tooth set of *Ptychodus atcoensis* (Elasmobranchii: Ptychodontidae), from the Cretaceous of Venezuela

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Abstract *Ptychodus atcoensis* is a characteristic Late Cretaceous durophagous shark, with a fossil record that was previously known exclusively from the Coniacian Atco Formation in Texas, USA, North America. We illustrate and describe for the first time a partial articulated tooth set of *P. atcoensis*, from the Cretaceous of the Venezuelan Andes, representing the only known record of this species outside of North America, thus significantly increasing the palaeobiogeographic distribution of this taxon. This partial tooth set also documents characteristic variation in the teeth of *P. atcoensis* that will allow isolated teeth of the species to be more readily identified and located in the dentition.

Keywords Cretaceous · Venezuela · Elasmobranchii · Ptychodontidae · *Ptychodus*

Introduction

The genus *Ptychodus* Agassiz 1835, refers to a characteristic group of Upper Cretaceous sharks, with a chronostratigraphic distribution ranging from the Albian to the Campanian (Welton and Farish 1993; Johnson et al. 2002; Cappetta 2012). The distinctive characteristics of the genus *Ptychodus* teeth with a massive and strong crown adapted for crushing, suggesting that these sharks had a

durophagous diet based on molluscs (see e.g., Kauffman 1972; Cappetta 2012). The geographical distribution of the genus *Ptychodus* during the Late Cretaceous was global, currently known from a little over 20 fossil species with records in Africa, North America and South America, Asia, Australia and Europe (MacLeod 1982; Williamson et al. 1989, 1991; Welton and Farish 1993; Antunes and Cappetta 2002; Brito and Janvier 2002; Mutter et al. 2005; Alvarado-Ortega et al. 2006; Blanco-Pinion et al. 2007; Hamm and Cicimurri 2011; Carrillo 2009; Underwood and Cumbaa 2010; Verma et al. 2012; Cappetta 2012; Carrillo-Briceño 2012a). The systematic position of *Ptychodus* is still highly uncertain. Characters like the dental morphology, the pavement pattern of the dentition and the presence of calcified vertebrae led many authors to suggest the inclusion of these sharks within Neoselachii (Maisey et al. 2004) or in specific groups like the Myliobatidae (Woodward 1889; Leriche 1902; Romer 1945), hybodontiformes (Welton and Farish 1993; Cappetta 2012) or Heterodontiformes (Müller 2008). *Ptychodus atcoensis* Hamm 2009 is the most recently described species of *Ptychodus*, and so far, known only from the Coniacian Atco Formation of north-central Texas in the United States of America. Here, we describe and illustrate a partial articulated tooth set of *P. atcoensis* from Cretaceous rocks of the Andes in Venezuela (Fig. 1), which was first illustrated by Aguilera (2010) as *Ptychodus* sp. This is the first record of *P. atcoensis* outside of Texas and thus palaeobiogeographic implications of this new record are discussed.

Materials and methods

In this study, we examined a piece of an articulated tooth set of *P. atcoensis*, for which the only existing locality data

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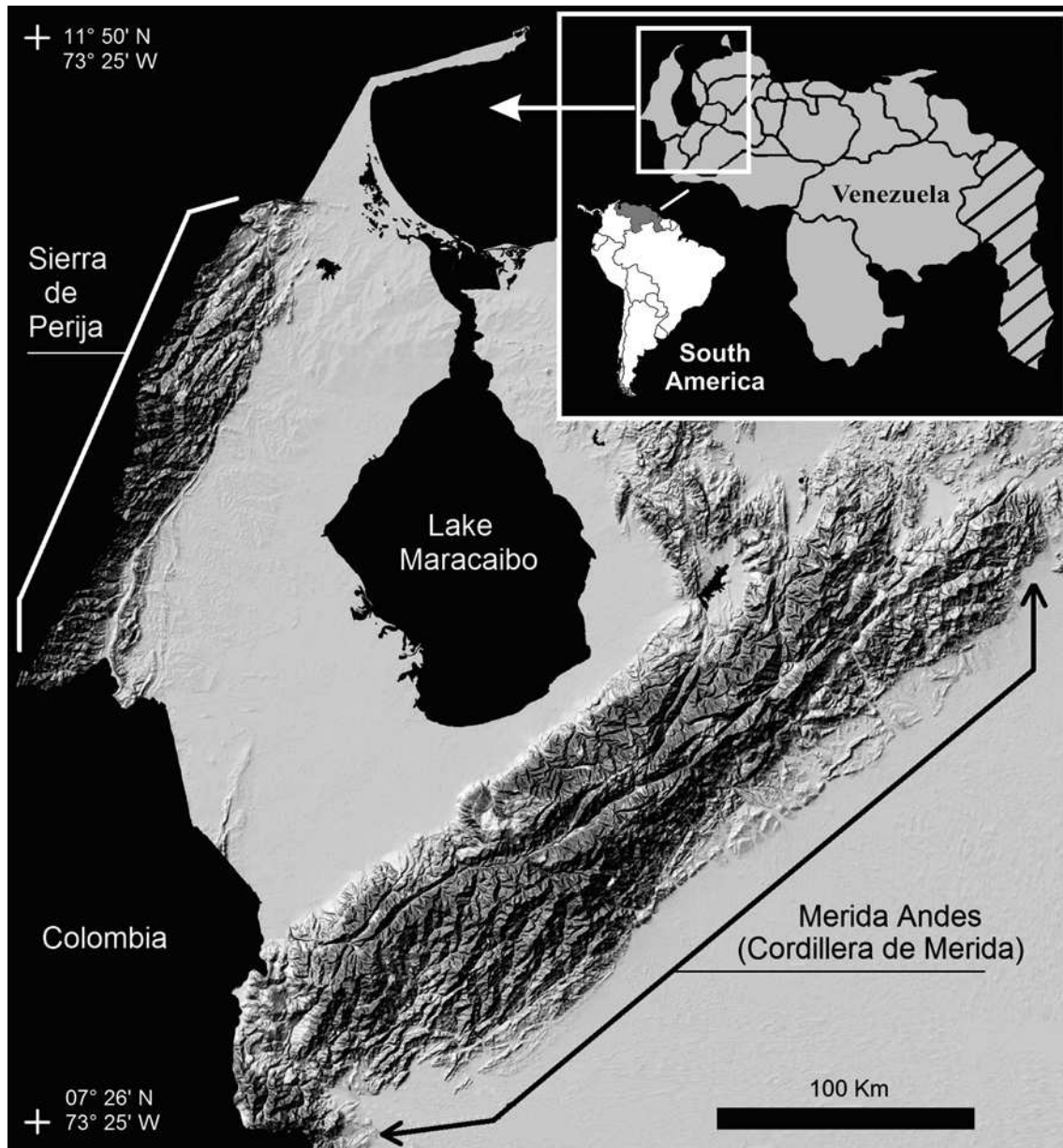


Fig. 1 Map of the Andes of Venezuela (modified from Garrity et al. 2010)

indicate the fossil came from Cretaceous rocks of the Andes in Venezuela, specifically in the Andes of Merida, but the geological formation and the exact location of the find are not recorded. This specimen is deposited in the Paleontology Collection of the Archaeological Museum Gonzalo Rincón Gutiérrez, Universidad de Los Andes, Mérida, with a repository code CU-010. This articulated tooth set is represented by 44 teeth, some of which are fractured and only preserve the marginal part of the crown. The tooth set is included in a single block with a very

indurated limestone matrix, and it is curved in the anterior section, which is due to taphonomic processes that affected fossilization; this does not allow the specimen to be observed in its entirety in occlusal view, as seen in other dentitions known for *Ptychodus* (see e.g., Shimada 2012). The taxonomic description and descriptive terminology have been adopted from Cappetta (2012), and the comparative material used for this study is located at the Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas (SMU).

Systematic palaeontology

Class Chondrichthyes Huxley 1880

Order *incertae sedis*

Family Ptychodontidae Jaekel 1898

Genus *Ptychodus* Agassiz 1835*P. atcoensis* (Hamm 2009) (Figs. 2, 3).1974 *Ptychodus* sp.; Meyer, p. 71–72.1993 *Ptychodus* sp.; Welton and Farish: p. 70.2009 *Ptychodus atcoensis*; Hamm: p. 63–65, Figs. 10 and 11.2010 *Ptychodus* sp. Aguilera: p. 11.2011 *Ptychodus atcoensis* Hamm and Cicimurri: p. 110, Fig. 3b.

Taxonomic comment

Hamm and Cicimurri (2011) claimed to propose the name *P. atcoensis* as a new species, noting that Hamm (2009) had already published the name in volume 8 of the Occasional Papers of the Dallas Paleontological Society. They state (Hamm and Cicimurri 2011, p. 111) that “because

this volume of occasional paper was not distributed through a publication house, according to ICZN code 8 regarding the dissemination of works where new taxa are named, herein we establish the taxon *P. atcoensis*.” However, our reading of Article 8 (especially 8.1) of the ICZN indicates that Hamm (2009) does meet the criteria of publication of the ICZN. Therefore, we attribute the species name *P. atcoensis* to Hamm (2009), not to Hamm and Cicimurri (2011).

Description

The tooth set (CU-010) belongs to a lower jaw and is composed of a symphyseal tooth file, a tooth file on the left side and three tooth files on the right side. The symphyseal tooth file is composed of 14 teeth, and these are the largest amongst the complete teeth of the tooth set; the largest specimen is 24 mm in length mesio-distally, 18 mm in width labio-lingually, and the crown is 20 mm high measured from the base of the enameloid. These teeth are symmetrical and nearly square in outline with tall central cusps with high and bulbous crowns where strong ridges oriented mesio-distally converge towards the apexes of the

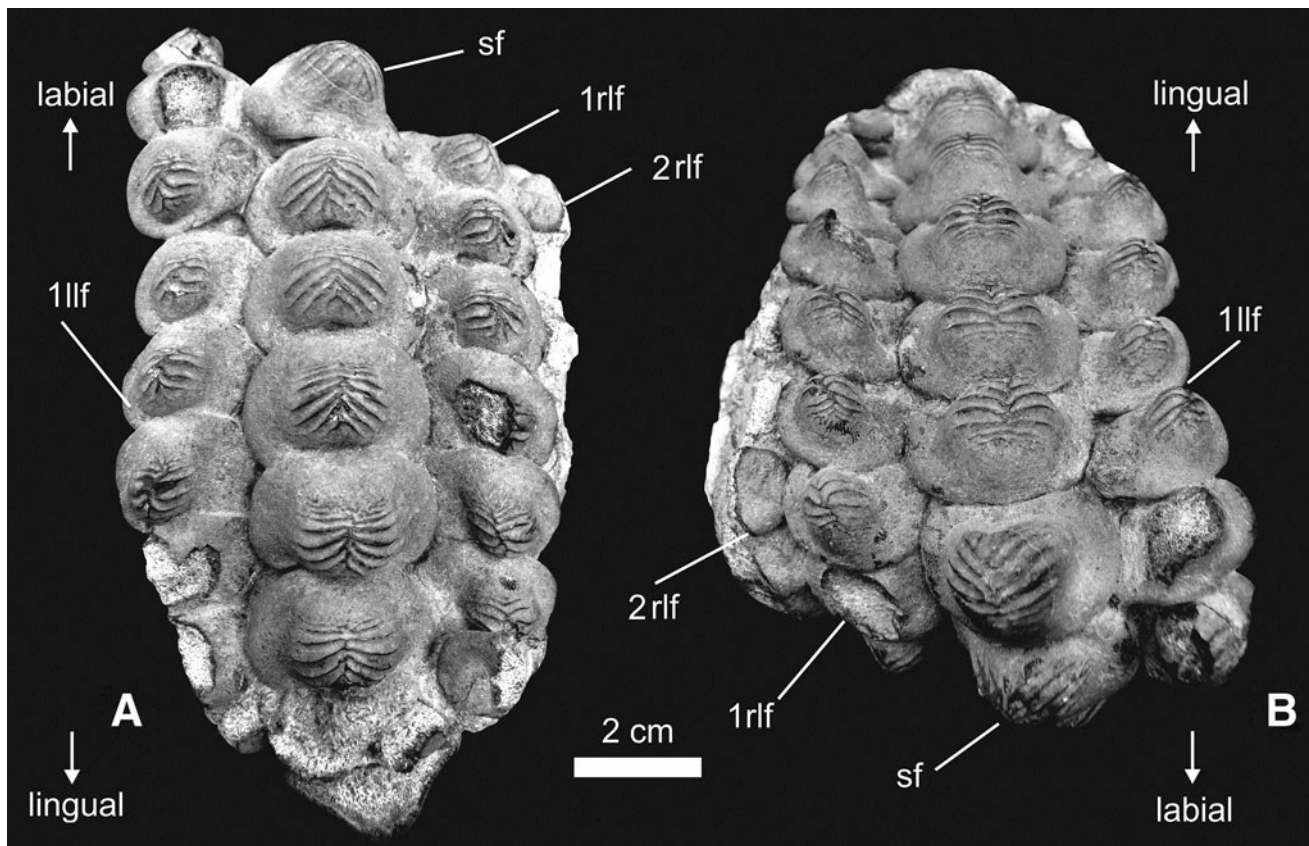


Fig. 2 Partial tooth set from lower jaw of *Ptychodus atcoensis* (CU-010). **a** Specimen in occlusal view. **b** Specimen in labial view. Anatomical abbreviations: *sf* symphyseal tooth file, *1llf* first left lateral tooth file, *1rlf* and *2rlf* first and second right lateral tooth file

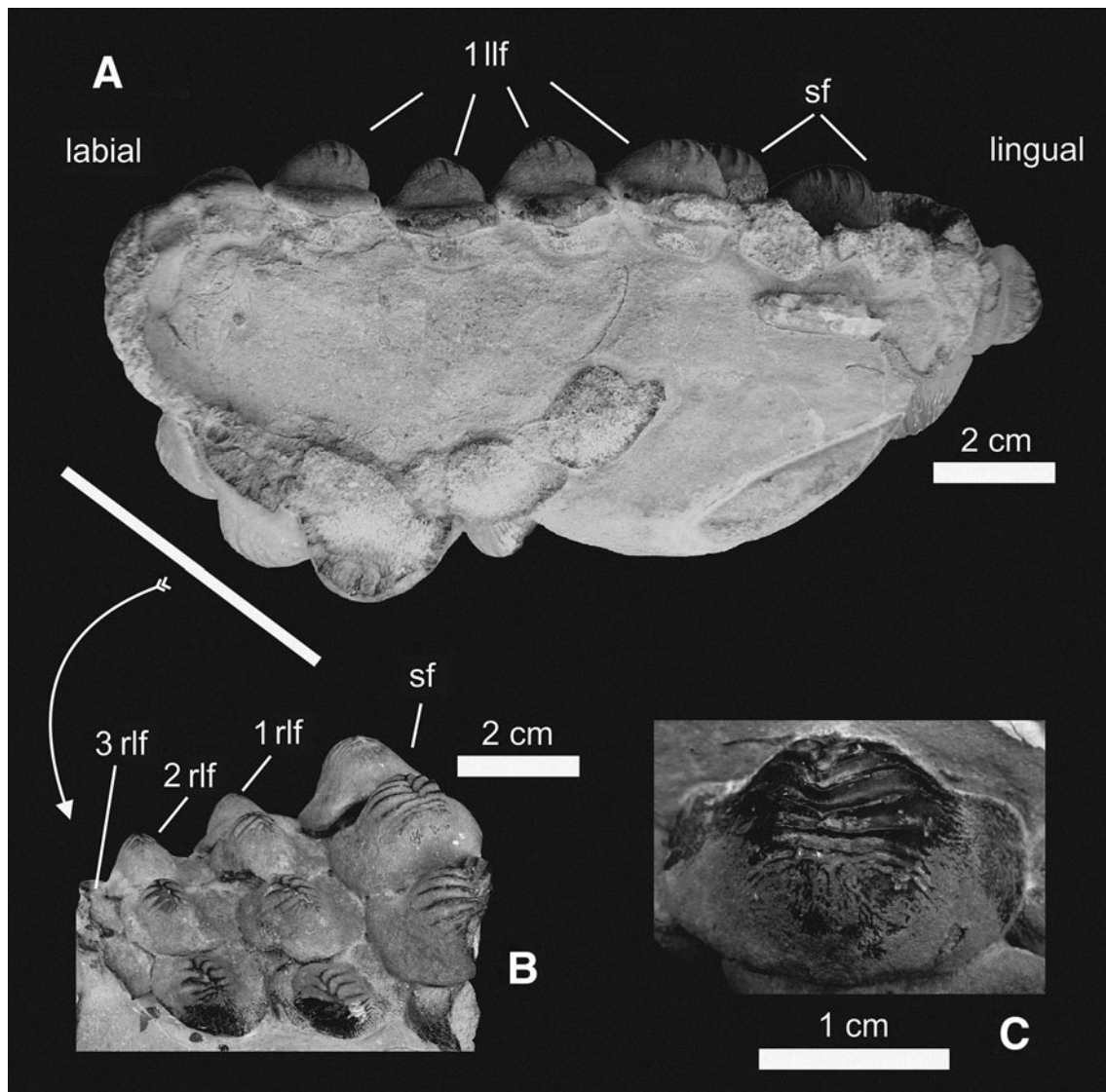


Fig. 3 Partial tooth set from lower jaw of *Ptychodus atcoensis* (CU-010). **a** Specimen in distal view. **b** Lateral tooth files of the right side. **c** Symphyseal tooth in occlusal view. Anatomical abbreviations: *sf*

symphyseal tooth file, *llf* first left lateral tooth file, *1rlf*–*3rlf* first to third right lateral tooth file

crowns to create a distinctive chevron pattern. These ridges are thick at the base and thin at the apex, creating a cutting edge, which is maintained from the apex of the crown to the marginal area of the tooth. The marginal area is fully ornamented by concentric ridges and a strongly granular texture. The labial rim of the crown is convex and constitutes the point of articulation (articular facet) to the lingual face of a tooth located immediately labially. The lingual rim is concave with a shallow depression at the base of the crown for an articulation with the margin of the labial rim of the tooth positioned immediately lingually. The mesio-distal margins are wide and rounded.

The first lateral tooth file at the left and right side of the tooth set (CU-010) has 9 and 12 teeth, respectively, and the

second tooth file of the right side only has 3 complete teeth and 3 left marginal crown fragments. At the right side of the tooth set, there is a third tooth file; however, this only has 3 left marginal parts of the crowns.

All these lateral teeth have an asymmetrical shape, with a crown more rounded and a central cusp canted (or offset) laterally. Ridges on the central cusp tend to converge toward the crown center but do not cross the crown as transverse ridges. The marginal area is fully ornamented by concentric ridges and a strongly granular texture, and at the lingual rim there is a shallow depression at the base of the crown, for an articulation (articular facet) with the margin of the labial rim of the tooth positioned immediately lingually. The basal section of all teeth is covered by (encased

in) the limestone matrix, and for this reason the root features cannot be observed.

Discussion

Species included in the genus *Ptychodus* can be differentiated on the basis of differences in dental morphology. According to Hamm and Shimada (2004), the main criterion for the identification of species within *Ptychodus* is the determination of distinctive features such as the crown height, configuration and number of ridges present in the crown and the ornamentation of the marginal area. *P. atcoensis* was known previously from the Coniacian of Texas, USA, for more than 25 years before the species was formally named by Hamm (2009). This very distinctive species is a high-crowned *Ptychodus* most readily recognized by the chevron-shaped transverse ridges on the cusp apices (Welton and Farish 1993; Shimada et al. 2009; Hamm 2009; Hamm and Cicimurri 2011). According to Hamm and Cicimurri (2011), the dental morphology of *Ptychodus anonymus* Williston 1900 and *Ptychodus mammillaris* Agassiz 1835, which bears a similarity to *P. atcoensis*, can be clearly distinguished due to the characteristic chevron pattern present in *P. atcoensis*, among the diagnostic features that can also be used to differentiate this taxon from other species of the genus *Ptychodus* (Hamm 2009; Hamm and Cicimurri, 2011).

Meyer (1974) suggested that *P. atcoensis* is a taxon transitional between *P. anonymus* and *Ptychodus mortoni* Mantell 1839. However, the suggestion of Meyer (1974) is not likely given that *P. anonymus* has a Cenomanian–Turonian range (Welton and Farish 1993), and *P. mortoni* ranges from the early Turonian to the Campanian (Shimada 2012), both species older than *P. atcoensis*, which is probably restricted to the Coniacian of North and South America.

The morphological pattern of *P. atcoensis* has been recognized as similar to the pattern present in ptychodontid species, especially those with high crowns and radial ridges, such as *P. mortoni*, *Ptychodus cyclodontis* Mutter et al. 2005, and *Ptychodus* sp. described by Brito and Janvier (2002) and Carrillo (2009). *P. mortoni* has a heterodont dentition and its teeth have more conical crowns with a pattern of ridges radiating from the apex of the crown to the marginal area (Cappetta 2012; Shimada 2012) that differs from *P. atcoensis*, which presents a more rounded crown and a characteristic pattern of chevron-shaped ridges. *P. cyclodontis* was described from the Turonian of Cuba on the basis of a partial tooth plate and its dentition consists of teeth characterized by a high, robust conical crown with radial ridges (Mutter et al. 2005). The dental morphology

of *P. cyclodontis* is closely similar to that of *Ptychodus* sp. described by Brito and Janvier (2002), from the Turonian of Colombia or Venezuela; both taxa are homodont and can be considered conspecific (Mutter et al. 2005). The teeth of *Ptychodus* sp. described by Carrillo (2009) from the Cenomanian–Santonian (?) of Venezuela has an exceptional high conical cusp, a morphology that differs from *P. cyclodontis* and *P. mortoni*, but it is similar to *P. cyclodontis* in that it possesses a limited area in each tooth crown (Shimada 2012). Teeth of *P. atcoensis* possess more marginal area than the teeth of *P. cyclodontis* and *Ptychodus* sp. described by Carrillo (2009) (Shimada 2012). According to Shimada et al. (2009), whether or not the four *Ptychodus* species with radial ridges known at this time (*P. atcoensis*, *P. cyclodontis*, *P. mortoni*, and *Ptychodus* sp. described by Carrillo (2009)) constitute a monophyletic lineage cannot be ascertained because of the poor knowledge on some of the taxa.

Like other tooth sets of *Ptychodus*, the *P. atcoensis* tooth set from Venezuela is characterized by a symphyseal tooth file of relatively large teeth flanked by lateral tooth files of somewhat smaller teeth. Comparison with other illustrated tooth sets of *Ptychodus* (Woodward 1904; Williamson et al. 1991, Fig. 2; Hamm 2009, Figs. 4, 6, 8, 14; Shimada et al. 2009, Figs. 1, 2, 7; Shimada 2012, Figs. 1–5) reveals that the Venezuelan tooth set is part of the lower dentition, preserving the symphyseal tooth file flanked by lateral tooth files near the center of the mouth. Variation in the Venezuelan tooth set is characteristic of that seen in other tooth sets of *Ptychodus*: teeth of the symphyseal tooth file are more symmetrical and higher crowned than teeth of the lateral tooth files (see e.g., Hamm 2009; Shimada 2012). The high angle (about 90°) between the central cusp and flanking platform (relatively flat or sloping marginal area of the crown) is characteristic of the symphyseal tooth file in *P. atcoensis*, and these are robust and the largest teeth in the lower jaw, whereas the tooth sizes in successive lateral tooth files gradually decrease.

Previously, only isolated teeth of *P. atcoensis* were found at the base of the Coniacian Atco Formation (Austin Group) in Texas (Meyer 1974; Welton and Farish 1993; Hamm 2009; Hamm and Cicimurri 2011), which restricted their distribution to North America. The presence of *P. atcoensis* in the Cretaceous of Venezuela increases the palaeogeographic distribution of this taxon, but leaves a vacuum in terms of age, because there is no detailed record of the provenance of the Venezuelan specimen. The only Upper Cretaceous geologic units of the Andes of Venezuela of Coniacian age are La Luna Formation (Cenomanian–Campanian), with a wide distribution in the Mérida Andes (Cordillera de Mérida) and Sierra de Perija (Fig. 1), and the Navay Formation (Coniacian–Maastrichtian),

restricted to the southeastern flank of the Cordillera de Mérida (La Marca 1997). La Luna Formation is a unit with abundant vertebrate fossils (see Carrillo-Briceño 2012b), especially of fish, which includes the presence of *Ptychodus decurrens* Agassiz 1838, *P. mortoni* and *P. sp.* (Brito and Janvier 2002; Carrillo 2009; Aguilera 2010; Carrillo-Briceño 2012a). Given that the only previous record of *P. atcoensis* is of Coniacian age in North America, its Venezuelan record also could be inferred of Coniacian age with a possible source from La Luna Formation. However, no information about the geological formation and the exact location of the find are recorded.

Other records of *Ptychodus* from the Upper Cretaceous of South America include *P. whipplei* Marcou 1858, of the Itamaracá Formation, Brazil (Silva 2007), and *P. chappelli* from Colombia and Ecuador (Reinhart 1951; Wenz 1972). However, *P. chappelli* is likely an invalid species because its teeth are very similar to teeth of *P. mammillaris*. Relatively little is known of the distribution of *Ptychodus* species in the Gondwana continents during the Cretaceous. However, the record reported here and a recent record of *P. decurrens* from the Cretaceous of India (Verma et al. 2012) indicate a relatively cosmopolitan distribution of at least some *Ptychodus* species in seaways of both the northern and southern hemispheres. To test this idea, more records of *Ptychodus* need to be documented from South America, like that reported here, and from the other continents that made up Cretaceous Gondwana.

Conclusion

Based on comparisons between the CU-010 specimen, illustrated earlier by Aguilera (2010) as *Ptychodus* sp., and fossil material of *P. atcoensis* from the Coniacian Atco Formation in North America, we can confirm taxonomic allocation of the tooth set CU-010 to *P. atcoensis*. The specimen CU-010, though incomplete, is the only known record of a set of the articulated dentition of *P. atcoensis* and thus enables a clearer understanding of the morphology and pattern of dental articulation of this taxon. There is a lack of precise data on the geological unit and locality from which the specimen CU-010 was collected, leaving a void in terms of age and current knowledge of the chronostratigraphic range of *P. atcoensis*. However, its presence in the Upper Cretaceous of Venezuela significantly increases the palaeobiogeographic distribution of this taxon, as it represents the only known record of the species outside North America.

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